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Density effect on growth and metamorphosis of *Bufo stomaticus* larvae

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Bufo stomaticus larvae were reared at different active space (volume of water per tadpole), at various densities and controlled food levels in the laboratory. The growth curves were sigmoidal in every case. Although visual inspection of growth curves indicates higher larval growth rate with increasing active space up to a particular level, the data are not statistically significant. We conclude that available active space (range 63 ml to 500 ml per tadpole) has an insignificant effect on growth and metamorphosis of *B. stomaticus* larvae.

In our laboratory populations, mortality rate as well as absolute mortality were independent of initial density. The negative effect of density on larval growth rate is attributed to competition for food. Thus body mass is dependent significantly on initial density. Present findings show that initial density does not have significant effect on the time of metamorphosis except at very high density (320 tadpoles for 2.3 l of water), indicating that schooling tadpoles of *B. stomaticus* may be different from non-schooling tadpoles of *Rana*.

INTRODUCTION

Larval anurans are abundant in fresh water habitats during the rainy season in India. The larval period is important in anuran life history, as successful metamorphosis leads to the abundance of the adult toads and frogs. On the other hand, factors like drying of the water source, food shortage, predation, disease, and crowding, affect the successful metamorphosis of tadpoles.

Previous studies have shown a negative effect of density on growth rate and metamorphosis for anuran larvae due to competition for food (BROCKELMAN, 1969; DE BENEDICTIS, 1974), and other behavioural interactions (GROMKO et al., 1973; JOHN & FENSTER, 1975). BREDEN & KELLY (1982) found that "increased conspecific interaction may increase variation in the number of days to metamorphosis, therefore decreasing metamorphic synchrony and increased interaction increases mass at metamorphosis" among *Bufo americanus* tadpoles. GUYÉTANT (1970) has shown a positive influence of grouping upon growth and metamorphosis of *Alytes obstetricans* larvae and argued for the importance of physical factors of environment, like agitation and oxygenation of the water, on tadpole growth and survivorship. Many workers, e.g., BROCKELMAN (1969), WILBUR (1977), SMITH-GILL & BERVEN (1979), DASH & HOTA (1980), NAKATA et al., (1982), SEMLITSCH & CALDWELL (1982) and

MISHRA & DASH (1984), have shown that survival, successful metamorphosis and growth of larvae are density dependent to a large extent. TRAVIS (1983) found that survival in *Hyla gratiosa* tadpoles is a function of average body size in field enclosures.

In this paper we examine the effect of tadpole crowding and density on the growth and metamorphosis of *Bufo stomaticus* Lütken, 1863, which is commonly known as the marbled toad. This toad is found in India, Pakistan, Nepal, Sri Lanka and is abundant around the study site, Sambalpur University Campus, Sambalpur, Orissa. *Bufo stomaticus* is nocturnal but during the breeding season it can be found moving around during day time. In summer it estivates under ground to a depth of up to 1.22 meters (RAO, 1923). Usually solitary, non-breeding adults may aggregate in a jumbled heap when kept in captivity. Average sized adults measure 76 mm, snout-vent length. Juveniles are light brown while adults are of grey or olive colour. Sexually mature males have a bright yellowish coloration during breeding season. *B. stomaticus* breeds from mid-June to August, amplexing for a period of 1–4 days. Eggs are laid in two rows of translucent strings and the clutch size varies from 9000 to 11000. Generally eggs hatch after 24 h and the percentage of hatching depends greatly on the spreading pattern of egg strings in the egg deposit site. Tadpoles are small, black with silvery spots on the body.

MATERIALS AND METHODS

Adult male and female *B. stomaticus* were collected from the field during mid-June and kept in an animal care facility of our University for natural breeding. Eggs were collected on 24th June 1982 and allowed to hatch in polythene trays in laboratory condition (temperature 32°C–34°C). Larvae were mixed to create genetically similar populations at the start of the experiment. Tadpoles were reared in the laboratory in a natural photoperiod using polythene trays as culture pots. Tap water was conditioned with sodiumthiosulphate at a concentration of 8 mg/4.5 l (NACE & RICHARDS, 1972) and was used as culture medium. Water and food of each container was changed on alternate days.

A mixed diet was prepared by combining boiled *Amaranthus* sp. leaves, boiled egg yolk and cooked, minced goat meat in a ratio of 5:1:1 respectively. From the third day after hatching mixed food was supplied at the rate of 3 g per tray for each density up to 6th day and the quantity was increased to 5 g from 7th day onwards. In the other experimental treatments 1 g of mixed food was given per tray, in all the sets, throughout the study.

Two experiments were carried out : (1) In order to find out the effect of active space (volume of water per individual) on growth and metamorphosis, 10 larvae per tray were reared in polythene containers of four different diameters (17.5, 20.0, 26.5 and 34.0 cm) as well as in larger glass aquaria (59×30×30 cm), each with three replicates. The water depth was maintained at 2.5 cm deep in all the containers so that the total volumes were 630, 820, 1350, 2600 and 5000 ml respectively. The mass of all the individuals of a replicate tray, at one time, was determined (to 1 mg precision) to ascertain the mean growth rate. (2) To analyse the density effect on larval growth and metamorphosis, populations of six densities (10, 20, 40, 80, 160 and 320 tadpoles per tray) of *B. stomaticus* larvae were reared in polythene trays (diameter = 26.5 cm) with 2.3 l of conditioned water, each with three replicates. The mass of a sample of 10 tadpoles at a time were determined (1 mg precision) to ascertain the growth rate. The mean growth rate per individual was calculated from the three replicates. Metamorphosed individuals (defined as a tadpole with at least one forelimb exposed) were removed from the population.

RESULTS

SPACE EFFECT

Keeping the number of larvae (10) and water depth (2.5 cm) constant, we have increased the active space per individual simply by raising tadpoles in trays of different diameter. A mixed model analysis of variance (MORRISON, 1976) was used to examine the main effect of active space adjusted for time. The analysis (Table I) showed an insignificant 'F' value indicating that growth rate was independent of active space. Multiple regression analysis of body mass at metamorphosis with time as a covariate yielded the regression line:

Table I. – Analysis of variance of body mass of *Bufo stomaticus* larvae as a function of active space.

Active space per individual in ml	Time in days	Mean body mass (mg) : Sample size in parentheses		
		Block		
		1	2	3
63	7	70.3 (10)	72.2 (10)	71.9 (10)
	9	117.5 (10)	120.9 (10)	111.3 (10)
	11	153.0 (5)	170.4 (5)	153.8 (5)
82	7	85.5 (10)	78.0 (10)	81.2 (10)
	9	149.9 (10)	133.3 (10)	137.7 (10)
	11	199.0 (5)	179.0 (5)	182.6 (5)
135	7	95.1 (10)	96.4 (10)	96.4 (10)
	9	170.6 (10)	160.6 (10)	172.7 (10)
	11	221.4 (5)	212.6 (5)	221.0 (5)
260	7	111.9 (10)	109.7 (10)	118.4 (10)
	9	195.3 (10)	192.4 (10)	202.2 (10)
	11	239.6 (5)	241.4 (5)	250.2 (5)
500	7	110.0 (10)	103.7 (10)	113.9 (10)
	9	173.1 (10)	166.8 (10)	170.7 (10)
	11	240.6 (5)	225.0 (5)	231.8 (5)

Analysis of variance

Source	df	SS	MS	F	P (0.05)
Active space	4	27337.64	6834.41	2.34	ns
Block	2	179.93	89.97		
Active space × Block	8	679.81	84.98		
Error	30	100140.74	3384.02		
Total	44	128338.12	2916.78		

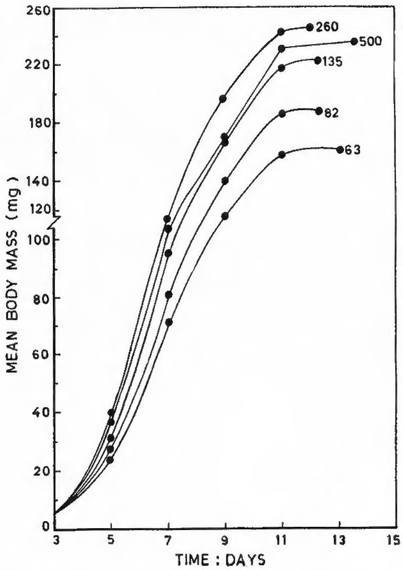

Fig. 1. – Active space dependent growth rate of *Bufo stomaticus* larvae. Numbers are active space/individual (ml).

M = 658.587 + (0.2136)AS + (−38.9265)t, (r^2 = 0.94, F =16.87, df = 2,2, ns, P> 0.05), where M = body mass at metamorphic climax, AS = active space per individual and t = average time (days) for metamorphosis; thus weight at metamorphic climax was independent of available active space, time being considered the covariate in the analysis. Based on this statistical analysis we conclude that active space had an insignificant effect on growth and metamorphosis of *B. stomaticus* larvae. However, visual inspection of growth curves (fig. 1) indicates that larvae generally grew better with increase in available active space as reflected in weight at metamorphosis, at least up to 260 ml active space per individual. The average growth rates, on the 9th day of development, were 116.6, 140.3, 168.0, 196.6 and 170.2 mg per tadpole in 63, 82, 135, 260 and 500 ml active space per individual, respectively.

CROWDING EFFECT

In the laboratory survival of amphibian larvae can be predicted by a non-linear model with normal error terms (WILBUR, 1976). Thus mortality rates were computed for our data using the equation:

$$N_t = N_o e^{-mt}$$

where N_t = number of larvae metamorphosed, N_o = initial density, m = mortality rate and t = average time (days) taken for metamorphosis. Table II gives the mortality rates and standard error of the mean from the data of three replicates. A visual inspection of these mortality rates and their standard errors suggested that mortality rate was not related to initial density of the population. However, results from BARTLETT's test showed that variances among the replicates at different densities were significantly heterogeneous (adjusted $\chi^2 = 24.37$, df = 5, $P < 0.005$), which rejected the hypothesis of homogeneity of slopes. This may indicate that mortality rate was independent of crowding.

Previous workers, like WILBUR (1977) and DASH & HOTA (1980), have found that the proportion of anuran larvae that metamorphosed to juvenile frogs was a function of initial

Table II. – Mortality rate in laboratory populations of *Bufo stomaticus* larvae.

Initial density	Mortality rate (regression coefficient ± SE)	Mean absolute mortality/replicate
10	0.00	0.00
20	0.00137 ± 0.00137	0.33
40	0.01456 ± 0.00763	6.67
80	0.00382 ± 0.00382	4.00
160	0.00027 ± 0.00027	0.67
320	0.00673 ± 0.00302	62.00

Table III. – Regression analysis of the natural logarithm of P_m (the proportion of population completing metamorphosis) on N_o (the initial density of the population).

Source	df	SS	MS	F	P(0.05)	Coefficient of determination
Regression	5	0.1513	0.03026	2.56	ns	52%
Residual	12	0.1416	0.0118			
Total	17	0.2929				

density and fitted a semilogarithmic model:

$$\ln P_m = -sN_o$$

where P_m = proportion of the population completing metamorphosis and N_o = initial density. The regression analysis (Table III) of $\ln P_m$ with N_o was not significant. Mean absolute mortality per replicate (Table II) showed that even though there was high mortality at the highest density (i.e., 320 tadpoles per tray), the number of individuals which died did not increase consistently with an increase in initial population density. WASSERSUG et al. (1981) were of the view that since *Bufo* larvae exhibit schooling behaviour they should exhibit less growth inhibition with crowding than do larvae of other genera (*Rana*, etc.). Results of this

Table IV. – Analysis of variance of body mass of *Bufo stomaticus* larvae as a function of initial density.

Initial density	Time in days	Mean body mas (mg): sample size in parentheses		
		Block		
		1	2	3
10	7	90.1 (10)	91.4 (10)	86.4 (10)
	9	161.6 (10)	168.3 (10)	151.7 (10)
	11	209.4 (5)	217.0 (5)	195.8 (5)
20	7	81.1 (20)	78.8 (20)	72.4 (20)
	9	137.8 (20)	142.6 (20)	128.6 (20)
	11	160.0 (10)	178.8 (10)	172.3 (10)
40	7	72.1 (40)	76.7 (40)	63.6 (40)
	9	117.7 (40)	123.4 (40)	113.2 (40)
	11	143.3 (15)	159.9 (15)	154.3 (15)
80	7	63.3 (60)	60.5 (60)	59.4 (60)
	9	92.2 (60)	91.0 (60)	97.3 (60)
	11	127.3 (15)	127.9 (15)	130.8 (15)
160	7	42.9 (80)	42.5 (80)	43.0 (80)
	9	66.8 (80)	66.2 (80)	66.2 (80)
	11	89.4 (20)	88.7 (20)	89.4 (20)
320	7	29.6 (100)	28.0 (100)	25.8 (100)
	9	41.7 (100)	44.1 (100)	41.4 (100)
	11	59.6 (40)	58.5 (40)	56.5 (40)

Analysis of variance

Source	df	SS	MS	F	P
Density (10, 20, 40, 80, 160, 320)	5	73562.99	14712.6	5.97	< 0.005
Block (1, 2, 3)	2	261.00	130.5		
Density × Block	10	382.33	38.23		
Error	36	56450.95	1568.08		
Total	53	130656.27	2465.23		

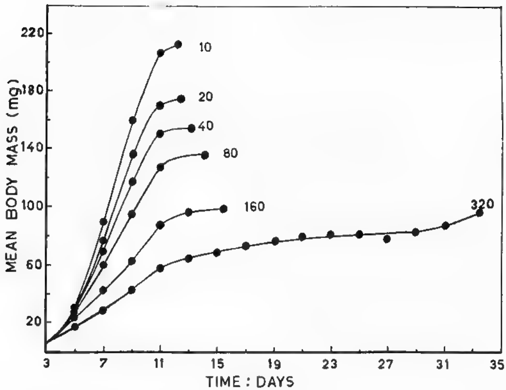

Fig. 2. – Density dependent growth rate of *Bufo stomaticus* larvae. Numbers are individuals per tray

investigation indicated that mortality rate as well as absolute mortality were statistically independent of initial density.

The mean body mass on the 7th, 9th and 11th days of growth were used in a mixed model analysis of variance (Morrison, 1976) to examine the main effect of initial density adjusted for the effect of time. The analysis (Table IV) showed that initial density had a significant effect ($P < 0.005$) on larval growth. Multiple regression analyses with available active space as the covariate of initial density were done to find out the effect of active space on larval growth on days 7th, 9th and 11th. The regression lines were described by the equations: $M = 67.9 + (-0.134)N_o + (0.102)AS$, ($r^2 = 0.99$, $F = 107.01$, df = 2,3, $P < 0.001$); $M = 105{,}48 + (-0.219)N_o + (0.263)AS$, ($r^2 = 0.97$, $F = 66.6$, df = 2,3, $P < 0.005$); and $M = 139.91 + (-0.276)N_o + (0.311)AS$, ($r^2 = 0.98$, $F = 126.88$, df = 2,3, $P < 0.001$) for days 7th, 9th and 11th respectively, where M = body mass per tadpole, No = initial density and AS = available active space per tadpole. The equations show that larval growth rate was dependent on initial density, but did not increase with the decrease of active space. The S-shaped growth curves (fig. 2) showed a right hand shift with crowding which suggests that growth rate of an individual was inhibited by the remaining members of the population.

Body mass at metamorphic climax was analysed by a multiple regression with time as a covariate of initial density. The regression line was described by the equation:

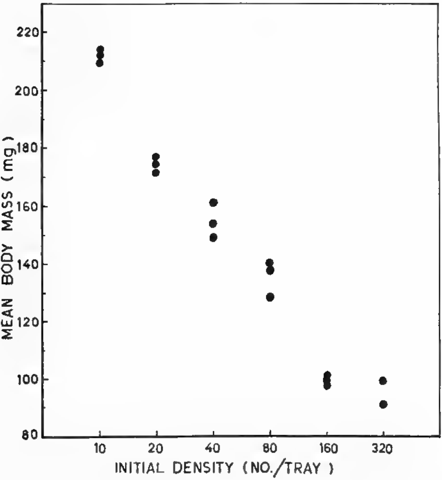

Fig 3. – Mean body mass at metamorphosis of *Bufo stomaticus* as a function of initial density of the population.

$M = 107.51 + (-0.783)N_o + (7.149)t$, ($r^2 = 0.89$, $F = 12.68$, $df = 2,3$, $P < 0.05$), where M = body mass at metamorphic climax, N_o – initial density and t = average time (days) taken for metamorphosis. This indicates that growth was dependent on initial density and was reflected in weight at metamorphosis but not on the time of metamorphosis, when time was considered as the covariate of initial density.

Regression of body mass at metamorphic climax on initial density with time as the covariate was highly significant. WILBUR & COLLINS (1973), DASH & HOTA (1980) and MISHRA & DASH (1984) suggested that metamorphosis is initiated only after a minimum threshold size is reached. The minimum threshold size observed in our experiment was 97.0 mg and the maximum size at metamorphosis was 212.3 mg (fig. 3). Body mass at metamorphic climax can be analysed from another angle, namely, larval growth was density dependent and body mass at metamorphosis was a reflection of growth rate. As there was a minimum threshold value, the larvae must grow for a definite minimum period in order to attain that necessary threshold weight. Hence time of metamorphosis is dependent on initial density. The actual values of time taken for metamorphosis in different densities (12.3, 12.5, 13.2, 14.2, 15.4 and 33.5 days in case of densities of 10, 20, 40, 80, 160 and 320 respectively) showed that time of metamorphosis increased with increase in initial density. However, this difference in time of metamorphosis was not statistically significant when time was considered as the covariate in the analysis up to the 160 density stage. Considering the statistical analysis and non-linearity of metamorphic time with initial density, it can be concluded that for *B. stomaticus* larvae, time of metamorphosis was independent of initial density up to a certain level. But at very high density (320 individuals per tray) time of metamorphosis was dependent on initial density (i.e., larvae had to grow for 33.5 days to attain the minimum threshold weight).

DISCUSSION

In this study the eggs came from a single local *B. stomaticus* population. Thus environmental and allelic heterogeneity among individuals was reduced. A greater proportion of the variance observed in the growth rate and metamorphosis can be accounted for by initial density of the populations in the experimental treatments.

More active space for tadpole means more of an oxygenated medium and hence an accelerated growth rate. Social interaction in aggregating toad tadpoles has a positive effect on metamorphic mass (BREDEN & KELLY, 1982). Beyond 260 ml of active space per tadpole, probably the social interaction among tadpoles was affected and hence a decline in growth has been observed. Visual inspection of growth curves (fig. 1) indicates that with an increase in active space tadpoles grew better up to a certain level (i.e., 260 ml active space per tadpole). Statistical analysis, however, showed that active space had an insignificant effect on larval growth.

Change in food level affected the larval growth in *Rana clamitans* (STEINWASCHER & TRAVIS, 1983) and in *Hyla gratiosa* (TRAVIS, 1984). But in the case of *Hyla chrysoscelis* food quality (protein to carbohydrate ratio) affected the larval growth (STEINWASCHER & TRAVIS, 1983). The "crowding effect" was attributed to production of a particular substance by larger tadpoles that inhibits the growth of smaller members of the population (RICHARDS, 1958). GROMKO et al. (1973) and JOHN & FENSTER (1975) have argued that behavioural interactions and their influence on hormonal control of growth account for the crowding effect. BROCKELMAN (1969) and WILBUR (1977) on *B. americanus* larvae, DASH & HOTA (1980) on *Rana tigerina* and MISHRA & DASH (1984) on *Polypedates maculatus* larvae interpreted the effect of density as the result of competition for food.

In the present study both available active space and food per individual decreased with increase in population density. Basing on the statistical analysis for the experiment on active space (Table I) we conclude that larval growth rate was more greatly affected by the increase in initial density than by the available active space. This is further supported by the multiple regression analysis of body mass on 7th, 9th and 11th day with available active space as the covariate of initial density; here it appears that body mass depended significantly on initial density, but not significantly on available active space. Analysis of variance (Table IV) shows that initial density had negative effect on larval growth rate. So we interpret the effect of

Table V. – Analysis of variance of body mass of *Bufo stomaticus* larvae as a function of initial density (lower density).

Source	Analysis of variance				
	df	SS	MS	F	P(0.05)
Density (10, 20, 40)	2	6862.37	3431.185	1.70	ns
Block (1, 2, 3)	2	555.683	277.842		
Density × Block	4	65.041	16.26		
Error	15	44948.287	2497.127		
Total	26	52431.381	2016.592		

density on growth rate as due to competition for food and more pronounced at high densities. This supports the findings of WILBUR (1977), DASH & HOTA (1980) and MISHRA & DASH (1984).

Schooling behaviour of aggregating tadpoles has been studied by many workers (WASSERSUG, 1973; WASSERSUG et al., 1981; BREDEN et al., 1982). NAKATA et al. (1982) were of the view that crowded tadpoles divide into two groups, a normally growing and a stunted group, when grown in a limited volume. The magnitude of such size sorting is species dependent and *Bufo* species show minimum size sorting (BREDEN et al., 1982). Increased conspecific interaction increases the time of metamorphosis for *Bufo americanus* (BREDEN & KELLY, 1982). Fig. 2 shows that time of metamorphosis increased with increase in density in our experiment. But the variation in time to metamorphosis is not statistically different up to a density of 160 tadpoles per tray. Therefore basing on the statistical analysis we conclude that in *B. stomaticus* larvae initial density has little effect on length of the larval period except at very high density (320 tadpoles per tray).

Bufo tadpoles generally school and for this reason one might expect that their growth might be less affected in nature by increased population density when compared with other non-schooling tadpoles, such as *Rana*. Results of the present study indicate that low densities (10, 20, 40 tadpoles per tray) do not affect larval growth rate significantly; indeed, Table V indicates that *Bufo* tadpoles differ from non-schooling tadpoles of *Rana*.

RÉSUMÉ

Des têtards de *Bufo stomaticus* ont été élevés dans différents "espaces d'activité" (volume d'eau par têtard), à diverses densités et avec des quantités contrôlées de nourriture. Dans tous les cas les courbes de croissance obtenues sont sigmoïdales. Bien que l'inspection visuelle de ces courbes laisse entendre que le taux de croissance larvaire augmente avec l'espace d'activité, les résultats ne sont pas statistiquement significatifs. L'espace d'activité, dans la fourchette de 63 ml à 500 ml par têtard, a donc un effet insignifiant sur la croissance et la métamorphose des têtards de *Bufo stomaticus*.

Dans nos élevages, le taux de mortalité ainsi que la mortalité absolue se sont avérés indépendants de la densité initiale. L'impact négatif de la densité sur le taux de croissance larvaire est attribué à la compétition pour la nourriture. Ainsi la masse corporelle dépend directement de la densité initiale. En revanche cette dernière n'a pas d'effet significatif sur la durée de la vie larvaire jusqu'à la métamorphose, sauf à de très hautes densités (320 têtards pour 2,3 l d'eau), ce qui suggère que les têtards de *B. stomaticus*, qui vivent groupés ("schooling"), sont peut-être différents à cet égard des têtards de *Rana* qui vivent non groupés.

(Résumé traduit par A. Dubois)

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